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Penk, Marcin R. ; Saul, Wolf-Christian ; Dick, Jaimie T.A. ; Donohue, Ian ; Alexander, Mhairi E.; Linzmaier, Stefan ; Jeschke, Jonathan M.

Published in:
Methods in Ecology and Evolution

DOI:
10.1111/2041-210X.12817

E-pub ahead of print: 20/05/2017

Document Version
Peer reviewed version

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Running title: An assessment framework for novel organisms

Word count: 6999

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Summary

1. The likelihood and impacts of invasions by novel organisms (e.g. non-native species, genetically-modified organisms) on the composition and functioning of receiving biological communities hinges on their capacity to exploit resources and/or avoid predation relative to resident counterparts. While assessment of invasion risk based on the comparison of functional responses (per-capita consumption rate as a function of resource density) of novel species with native analogues has been gaining popularity, it may be undermined if alternative prey and potential predators are not represented realistically.
2. Here, we propose a conceptual framework that enables rigorous identification of trophic traits conducive to invasion success by novel organisms – irrespective of their trophic position – and their likely ecological impacts, given their arrival and establishment. We focus on consumption here, but our framework can also be used for autotrophic energy acquisition, and extended to non-trophic and indirect interactions.
3. The framework enables a structured and prioritised selection of subsets of trophic links for invasion risk assessment. It is based on foraging theory and advances in comparative functional responses in invasion ecology. It can even be used in the absence of a resident comparator organism and when resources or predators are only partly known.
4. Our approach enhances the predictive power of species screening, and thus advances prevention and management of invasions under a common framework for all types of novel organisms.

Key-words: alien species, dietary generalism, ecological novelty, GMO, invasion success, functional responses, predator-prey trophic interactions, risk assessment

Introduction

Predicting biological invasions (i.e. the spread of non-native species beyond the point of introduction) and managing their impacts (i.e. quantifiable alterations of the receiving ecosystem) remain key challenges in ecology (Simberloff *et al.* 2013). This demands improved understanding of the mechanisms of invasions. Human-assisted species translocations entail transfers across barriers that limit natural dispersal, and thus between environments which can have substantially different eco-evolutionary histories. Thus, introduced organisms can impart a high degree of ecological novelty to a system, which is conducive to invasiveness (Saul, Jeschke & Heger 2013). Organisms arriving in new environments enter resident ecological interaction networks, and the identification of their interactions within resident communities is important for understanding community dynamics. Predicting the attributes of these novel interactions is crucial for prioritising management of existing and anticipated invasions, and for assessing the side effects of intended introductions. Novel organisms (including translocated, but also range-expanding, genetically modified, synthesised or resurrected organisms; Jeschke, Keesing & Ostfeld 2013), whose ecological traits contrast with the eco-evolutionary experience of their resident interaction partners (Saul & Jeschke 2015), can potentially transform resident interaction networks through, for example, altering strengths, spatio-temporal patterns or other functional attributes of interactions (Mitchell *et al.* 2006; Downing *et al.* 2012; Mayer *et al.* 2013; Penk, Irvine & Donohue 2015).

Predation is a particularly important interaction type that can have strong impacts on community dynamics. This is primarily because it affects both predator fitness and prey biomass directly, potentially causing trophic cascades (Terborgh & Estes 2010; O'Connor *et al.* 2013) and food limitations for competitors (Strayer & Malcom 2007). Introduced predators can therefore affect resident prey populations significantly (Hays & Conant 2007;

71 Strayer 2009; Downing *et al.* 2012), with efficient exploitation of resources being conducive
72 to high population growth, likely invasion success, and potentially considerable ecological
73 impacts. Resource density is a key determinant of the feeding rate, and this relationship is
74 characterised by 'functional response' curves (Holling 1959). For instance, decreasing prey
75 density can reduce predator encounter rates with prey and thus offer a density-dependent prey
76 refuge in a predator-prey system with a sigmoidal (i.e. Type III) functional response, but not
77 with alternative functional response shapes where high proportions of prey are killed at low
78 prey densities (Type I, II or their variants; Holling 1959; Jeschke, Kopp & Tollrian 2004;
79 Jeschke & Tollrian 2005). Thus, the height – in particular the maximum feeding rate (i.e.
80 curve asymptote) – and the shape of functional responses can reveal characteristics of
81 consumer-resource interactions that are important for community dynamics and composition.
82 Invading predators with high ecological impact on their prey populations often have
83 elevated functional responses compared to ecologically similar native species (Dick *et al.*
84 2017). Using comparative functional responses as an empirical screening method is thus
85 rapidly gaining popularity among invasion biologists (Dick *et al.* 2013; Alexander *et al.*
86 2014; Barrios-O'Neill *et al.* 2014a; Rosewarne *et al.* 2016; Xu *et al.* 2016). The method
87 typically infers invasion success and/or potential impacts from a limited number of prey
88 species (frequently just one). However, biological invasions tend to lead to replacement of
89 niche specialists by generalists (Clavel, Julliard & Devictor 2010), and numerous studies
90 have identified a positive association between dietary generalism and invasion success
91 (Bessa-Gomes *et al.* 2003; Jeschke & Strayer 2006; Romanuk *et al.* 2009; Clavel, Julliard &
92 Devictor 2010; Arbaciauskas, Lesutiene & Gasiunaite 2013, but see Cassey *et al.* 2004 and
93 Jackson *et al.* 2016). Thus, the inefficient use of one particular resident prey species does not
94 necessarily preclude invasion success or impact upon ecological networks with realistic
95 complexity. In other cases, a resident organism may be an inferior predator on a particular

prey species, and falsely appear a weaker overall interactor, compared to an introduced predator solely as a result of differing specialisation, despite apparent ecological similarity (Rosenfeld 2002; Dunoyer *et al.* 2014). Investigating functional responses with multiple prey, thereby taking into account the potential role of generalism and specialism, can buffer against such biases and at the same time improve the much needed representation of whole-ecosystem impacts of novel organisms (Ehrenfeld 2011; Simberloff 2011; Penk, Irvine & Donohue 2015). Furthermore, novel organisms can themselves be controlled by resident predators (Romanuk *et al.* 2009; MacNeil *et al.* 2013; Pintor & Byers 2015). Not accounting for top-down control experienced by introduced species, as has been typically the case in functional response-based screening methods, risks over-estimating their consumptive impacts and invasion success (but see Barrios-O'Neill *et al.* 2014b; Alexander, Raven & Robinson 2015).

Both top-down and bottom-up trophic interactions can thus directly affect the survival, fitness and ecological impacts of novel organisms. The complexity of these trophic links, including diet breadth and number of enemies, is an important determinant of invasion success (Romanuk *et al.* 2009). However, the logistics of incorporating multiple prey and predators into comparative functional responses may be demanding and frequently prohibitive.

We propose a conceptual framework for identifying and selecting a prioritised subset of trophic links to empirically identify the capacity for invasion success and ecological impacts of novel organisms (Fig. 1). We provide a worked example of the application of the framework for an intermediate consumer, the marbled crayfish (*Procambarus fallax* forma *virginalis*) in German low-land lakes (Fig. S1). This includes selection of both predators and prey, and can therefore instruct assessment of organisms of any trophic position. In addition, the marbled crayfish does not have any known native populations, and thus it is exemplary of

quite complex assessment scenarios. For clarity, our arguments relate to predation, which includes true predation, herbivory, parasitism and parasitoidism. However, detritivory can also be an important dietary subsidy of generalist consumers (Wise, Moldenhauer & Halaj 2006; Jackson *et al.* 2016) and should be carried through the assessment if it contributes to the diet of the novel ('focal') organism. Although we focus on consumption, our framework can be applied to autotrophic energy acquisition, and extended to non-trophic and indirect interactions. Whereas the non-empirical steps of our framework are readily applicable to any type of interaction, non-trophic interactions may require different empirical methods.

Mapping potential interaction partners in the target community

Unless interaction with a particular resident organism is an *a priori* focus of assessment, an initial step of comprehensively mapping a potential network of direct consumptive interactions of the focal organism in the receiving ('target') community should enable minimisation of selection biases that may impede realistic assessment of the impact of the novel organism. This can be achieved by first listing all partners in direct consumptive interactions of the focal organism in its established range. This is then followed by matching all resident organisms in the target community that conform to the archetypes of these interaction partners and are likely to at least partly share spatio-temporal distribution patterns with the focal organism (Fig. 1). We define an archetype as organisms that have a similar set of morphological and behavioural traits that can condition a given type of interaction (Cox & Lima 2006; Winemiller *et al.* 2015), for example, feeding or defence strategy.

Observed trophic interactions in a given environment may not fully represent the feeding preferences of an organism (Futuyma & Moreno 1988; Devictor *et al.* 2010), and trophic interaction strength with a particular prey may depend on its availability in comparison to other prey rather than on the true preference of the consumer (Jaworski *et al.*

2013; Davis *et al.* 2015; Hanmer et al. 2017), as well as on environmental drivers. Thus, interaction partners of the focal organism as well as interaction strengths may vary among communities that differ in species composition and densities. If the focal organism is already established in the target environment, site-specific data about interaction partners should be given precedence above data from other areas. Otherwise, information from multiple communities within the distribution range of the focal species may improve control for context-dependencies. Assigning preference attributes based on how frequent and dominant interaction partners are throughout the established range (e.g. Kissling *et al.* 2014) can then help prioritise the selection of interaction partners for assessment. Considering ontogenetic stages of the focal organism with contrasting interaction partners (e.g. size class, identity or trophic guild of prey or enemies) could further improve predictions because limitation at any single stage preceding reproduction could constrict population dynamics (Werner & Gilliam 1984; Rudolf & Lafferty 2011).

For focal organisms that do not yet occur in nature, such as genetically modified, resurrected, synthetic, hybridised or selectively bred organisms, interaction partners of phylogenetically or functionally closest ('quasi-focal') organisms may provide reasonable approximation. For example, the marbled crayfish, introduced recently to German freshwaters (Chucholl, Morawetz & Groß 2012), originated in the aquarium trade and does not have any known native populations (Vogt *et al.* 2015). However, it is morphologically and functionally similar to the spiny-cheek crayfish (*Orconectes limosus*), a well-established earlier invader in Germany which can be considered a quasi-focal organism. The spiny-cheek crayfish is an omnivore that feeds on benthic invertebrates and macrophytes, and itself falls prey to fish, waterfowl and mustelids. Interaction partners of the spiny-cheek crayfish are thus good candidate prey and predators of the marbled crayfish (Fig. S1).

Screening for a prioritised subset of the mapped interaction network

Should assessment be restricted to a subset of potential interaction partners, then criteria for selecting them depend on the goal of the assessment – invasion success, impact, or both (Fig. 1). The colonisation of areas beyond the point of introduction, synonymous with invasion success (Blackburn *et al.* 2011), is likely if an organism is able to utilise abundant resources, and/or if it can avoid high extrinsic mortality. Thus, we recommend focusing on potential resources with the highest biomass in the target ecosystem when selecting a prioritised subset of all identified potential interactions for the assessment of the likelihood of invasion. However, attention should also be paid to potential predators that are expected to have the highest predation pressure on the focal organism. Notably, high predation on the focal organism could come from consumers with high individual predation rates, or those that are not necessarily individually voracious but occur in high abundance (Dick *et al.* 2017).

Interactions of the focal organism with dominant predators and prey have the potential to affect major energy conduits within ecological networks and are thus conducive to strong ecosystem-level impacts, such as altered diversity, structure and functioning of target communities (Lockwood, Hoopes & Marchetti 2007; Penk, Irvine & Donohue 2015; Jackson *et al.* 2016). Further, interactions with keystone species or ecosystem engineers (Jones, Lawton & Shachak 1994; Power *et al.* 1996; Angelini *et al.* 2015), which are not necessarily very abundant, could amplify the indirect impact of invaders and convey ecosystem-level impacts. They should also be considered. It is also important to consider interactions with individual predator and prey organisms of conservation importance, regardless of whether such interactions have the potential to affect the whole community (Fig. 1).

In general, we advise selecting multiple prey and predator species of the focal organism for empirical assessment. However, their number and distribution among the interactor groups discussed above (i.e. those of highest biomass, keystone organisms and

196 ecosystem engineers, and those of conservation importance; Fig. 1), will depend on the
197 purpose of the assessment, trophic level and niche breadth of the focal organism, food web
198 complexity in the target ecosystem, management priorities and logistic constraints. For
199 example, monophagous and oligophagous predators, including parasites and parasitoids, have
200 inherently limited numbers of prey, while mesopredators typically have fewer predators than
201 basal prey (Turney & Buddle 2016). Figure 2 shows exemplary hypothetical module
202 structures for interaction settings between focal and resident organisms, indicating the
203 diversity of interactions that need to be considered. Some of the interactor group categories
204 will frequently overlap, and some may not be present in the target community. If the focal
205 organism is already established, experimental trials or field data can be used to ascertain and
206 prioritise interaction partners in the target community before engaging in full assessment.
207 Empirical examples of structured choices of prey in functional response studies of
208 invasive species are rare (but see Dick *et al.* 2013; Barrios-O'Neill *et al.* 2016; Xu *et al.*
209 2016). In our worked example of the marbled crayfish (Fig. S1), the mussel *Dreissena* spp.
210 has high abundance in the target community and is an ecosystem engineer. Dreissenids and
211 other animal prey with poor escape response are key and preferred contributors to crayfish
212 energy budgets (Momot 1995). The snails *Radix* spp. and *Bithynia tentaculata* are other
213 important primary consumers in the target community that are readily consumed by crayfish
214 (Olsen *et al.* 1991; Nyström, Brönmark & Granéli 1999). Testing predation on these three
215 mollusc taxa could thus inform the assessment of both invasion success and ecological
216 impacts of the marbled crayfish (Figs. S1 and S2). The quasi-focal organism (spiny-cheek
217 crayfish) is a major prey of perch (*Perca fluviatilis*), which is a relatively abundant fish
218 species in German low-land lakes and often holds key positions in food webs (Persson,
219 Bystrom & Wahlstrom 2000). Predation by perch is likely restricted to immature or post-
220 moult crayfish because of gape size limitation and the formidable defences of mature

221 crayfish. Nonetheless, this predatory fish could depress crayfish population dynamics, and
222 thus it is a potentially important interactor (Figs. S1 and S2).
223
224 **Empirically testing trophic interactions for the prioritised interaction subset**
225 Introduction of an organism that is of a predator or prey archetype already present in the
226 resident community implies that resident prey or predators, respectively, are likely already
227 familiar with such an archetype (Saul & Jeschke 2015). Because of such experience, it can be
228 assumed that a novel organism can impact resident prey populations more strongly than their
229 currently experienced predation pressure if its predatory traits toward a particular prey
230 archetype are superior relative to its resident analogues. Similarly, a novel organism risks
231 high impact from resident predators if its defences are weaker than those of its resident
232 analogues, thus promoting prey switching. Therefore, comparing the trophic interaction
233 strengths of the focal organism with its prey or predators, with those of an ecologically
234 similar resident, where such exists, provides a useful benchmark for gauging the magnitude
235 of interaction strength (van Kleunen *et al.* 2010; Dick *et al.* 2014). By definition, no two
236 species are identical (Ordonez 2014), but resident organisms that are of the same predator or
237 prey archetype (Cox & Lima 2006; Winemiller *et al.* 2015) can offer a useful approximation
238 of a reference baseline if any relevant functional differences between otherwise analogous
239 species are acknowledged. In our worked example, the marbled crayfish co-occurs with other
240 omnivorous crayfish (Chucholl, Morawetz & Groß 2012) of a similar predator and prey
241 archetype that can be used as comparators (Fig. S1).
242 On the other hand, a novel organism that does not have any resident comparator is
243 likely to have characteristics largely unfamiliar to resident prey and predators and thus the
244 potential to bypass their defences and offences (Saul & Jeschke 2015). In such a case, the
245 absolute, rather than comparative interaction strength of the focal novel organism with its

246 prey and predators can be of primary interest, and offtake rate of prey in relation to its
247 reproductive rate can be used to predict impact on prey populations (MacNeil *et al.* 2013;
248 Fig. 1). Qualitative pilot experiments can inform which degree of functional similarity can be
249 assumed as a baseline.
250
251 **Inference to real ecosystems**
252 *In situ* measurements and manipulations provide realistic settings, but tend to allow poor
253 control of confounding factors (but see Barrios-O'Neill *et al.* 2014a). Also, they cannot be
254 carried out if the focal organism is not (yet) present in the target environment. Laboratory
255 experiments, on the other hand, typically simplify biotic and abiotic contexts, and the applied
256 relevance of their results depends on the degree to which experimental settings facilitate
257 natural offensive and defensive behaviour. For example, sheltering or camouflage may alter
258 the shape of density-dependent predation, in that individual organisms devoid of their typical
259 protective settings during experiments are more exposed to predation (Whittingham &
260 Markland 2002; Horppila *et al.* 2003; Alexander, Dick & O'Connor 2013; Barrios-O'Neill *et*
261 *al.* 2015). Both ambient temperatures and environmental hypoxia can also affect activity
262 level, and moderate predator-prey interactions (Englund *et al.* 2011; Laverty *et al.* 2015; Penk
263 *et al.* 2016). Laboratory-derived functional responses typically isolate an individual predator
264 and single prey species (e.g. Dick *et al.* 2013; Barrios-O'Neill *et al.* 2014a; Xu *et al.* 2016,
265 but see Alexander, Dick & O'Connor 2013; Medoc, Spataro & Arditi 2013; Wasserman *et al.*
266 2016), and thus rarely account for prey switching or interference among predators which
267 could affect the outcome of an interaction (Amarasekare 2002; Tschanz, Bersier & Bacher
268 2007; van Leeuwen *et al.* 2013). The degree of spatio-temporal overlap of habitat use by the
269 focal organism and its interaction partners is another important consideration (Polis,
270 Anderson & Holt 1997). For example, a potentially strong interactor may have only a small

time window for realising such interactions if it rarely encounters particular prey and predator species. Whereas detailed propositions for ameliorating these problems are beyond the scope of this manuscript, we emphasise that lack of their consideration can undermine inference.

On the other hand, the need to quantify absolute interaction strengths accurately is circumvented in comparative studies, which focus on consumption rates relative to a native analogue rather than on absolute values, with an underlying assumption that both comparators would be influenced similarly by experimental artefacts (Dick *et al.* 2014). Indeed, comparative functional responses derived from simple laboratory experiments can be highly successful in explaining real-ecosystem ecological impacts of invaders across taxonomic and trophic groups (Dick *et al.* 2017). Context-dependencies may thus be particularly influential in making inference from studies on a novel organism that does not have a resident comparator because they rely on quantification of absolute interaction strengths.

Our framework specifically focuses on biological interactions, but the importance of intrinsic characteristics of the novel organism also has to be considered. For example, prognoses of population and community dynamics require at least some information on the reproductive rates of the focal organism and its interaction partners. The reproductive rate of a consumer determines the degree to which it can capitalise numerically on its ability to exploit prey and cumulatively increase its impact on prey populations, whereas the reproductive rate of prey determines their capacity to persist under given predation pressure (Twardochleb, Novak & Moore 2012). Both of these factors are key drivers of community dynamics.

Any model necessitates a trade-off between generality, realism and precision (Levins 1966). It is impossible to achieve all of these simultaneously to full extent, and the decision as to how to optimise this trade-off depends upon the focal system. We therefore present a

296 basic framework here, which needs to be adjusted and extended on a case-by-case basis to
297 make it useful for the particular focal system in question. For example, for many systems it
298 will be useful to incorporate non-consumptive or indirect interactions, or impacts on
299 ecosystem services into the basic framework.
300
301 **Non-consumptive and indirect interactions**
302 Consumptive interactions are the key focus of our framework (Fig. 1). However, non-
303 consumptive and indirect (trait-mediated) interactions, for example through interference,
304 facilitation and inhibition, can have important implications for community dynamics and in
305 some cases even take prominence over direct impacts (Suraci *et al.* 2016). Indirect
306 interactions occur when one species alters the effects that another species has on a third,
307 potentially confounding predicted impacts of a novel organism that are derived from two-
308 species studies (White, Wilson & Clarke 2006). For instance, changes to the foraging
309 behaviour of a resident intermediate consumer as a result of the presence of a novel higher-
310 order predator may alter the strength of interactions with a basal prey resource, releasing it
311 from predation pressure (Townsend 1996). Alternatively, the presence of a resident higher-
312 order predator may result in an exacerbated effect of a non-resident intermediate species
313 towards its prey in comparison to a resident consumer, again influencing impact of the focal
314 organism (Barrios-O'Neill *et al.* 2014b). Quantification of beneficial and disadvantageous
315 outcomes of such interactions, in particular regulation of feeding and mortality rates, could be
316 readily integrated in the empirical steps of our framework.
317
318 **Conclusions**
319 Key theoretical progress on functional responses in invasion ecology has come from
320 retrospective empirical attempts to explain invasion success and impacts of established

321 invaders (Hooff & Bollens 2004; Radford, Dickinson & Lord 2007; Bollache *et al.* 2008;
322 Dick *et al.* 2013). Such attempts typically focus on isolated interactions in which the invader
323 is clearly efficient and superior over a native comparator. However, biological invasions are
324 highly dependent on biological contexts (Donohue *et al.* 2013; Ricciardi *et al.* 2013; Saul,
325 Jeschke & Heger 2013), and robust prospective applications require a more comprehensive
326 assessment network with multiple interaction partners, including predators of the focal
327 organism. Applications of functional responses in biocontrol frequently fail to explain impact
328 on individual prey organisms (Lester & Harmsen 2002; Fernández-Arhex & Corley 2003).
329 The inclusion of predators and alternative prey, together with more realistic representation of
330 key abiotic conditions and explicit discussion of the relevance of results to natural
331 ecosystems can improve explanatory and predictive power of impact assessments. We
332 focused here on predation in a broad sense, but the same assessment protocol and analogous
333 empirical methods can be used for detritivorous and autotrophic energy acquisition (Radford,
334 Dickinson & Lord 2007; McNickle & Brown 2014).
335 Risk assessment based on performance in comparable environments, where such
336 information exists, is less laborious than collecting new data. However, interaction partners in
337 new and existing ranges should be compared in a structured way to minimise bias. The steps
338 of our framework that are based on existing data can be used to inform such comparisons
339 (Fig. 1). Furthermore, novel organisms can be introduced to dissimilar communities or
340 abiotic conditions in comparison to their existing ranges, or they can be absent in nature.
341 Such scenarios preclude comparisons based on performance elsewhere and necessitate
342 collection of new data (Fig. 1). In the face of limiting resources, a compromise between
343 experimental complexity and accuracy of risk assessments needs to be reached on a case-by-
344 case basis. Notably, relevant empirical data can be collected *in situ* (Angerbjorn, Tannerfeldt
345 & Erlinge 1999, Goss-Custard *et al.* 2006; Moustahfid *et al.* 2010, Barrios-O'Neill *et al.*

2014a), permitting empirical testing of organisms that do not lend themselves well to laboratory conditions, or should not be interfered with on ethical grounds. In any case, the broader interaction network in the focal ecosystem should be at least theoretically considered, even if just to critically scrutinise the assessment outcomes. The non-empirical steps of our framework can inform such exercises regardless of the scale or complexity of the system in question.

Acknowledgments

We appreciate helpful comments by the Associate Editor and two reviewers. MP was supported by a COST Action TD1209 STSM grant (011015-062070). WCS and JMJ were supported by the ERA-Net BiodivERsA (project FFII) with Deutsche Forschungsgemeinschaft (DFG; JE 288/7-1). JMJ was additionally supported by the DFG grant JE 288/9-1.

Data Accessibility

This manuscript does not include any data.

Author contributions statement

MP, WCS and JMJ conceived key ideas; MP led the writing of the manuscript; all authors contributed critically to the drafts.

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Supporting Information

Fig. S1. Illustration of predator and prey selection using an example of the marbled crayfish.

Fig. S2. Illustration of an interaction module structure for testing, using an example of the marbled crayfish.

Figure captions

Fig. 1. Framework for quantifying interaction strength of a focal organism with multiple resident organisms in the target community for a given type of interaction. Nodes and broken links indicate alternative and supplementary paths, respectively. *S* and *I* indicate interaction-partner categories relevant for the assessment of invasion success and ecological impacts, respectively.

Fig. 2. Hypothetical interaction module structures for testing trophic interactions of a focal organism (oval shapes) representing top (a, b), intermediate (c, d) and basal (e) trophic positions, and two extrema on the diet-breadth continuum (polyphagous [a, c] and monophagous [b, d]).

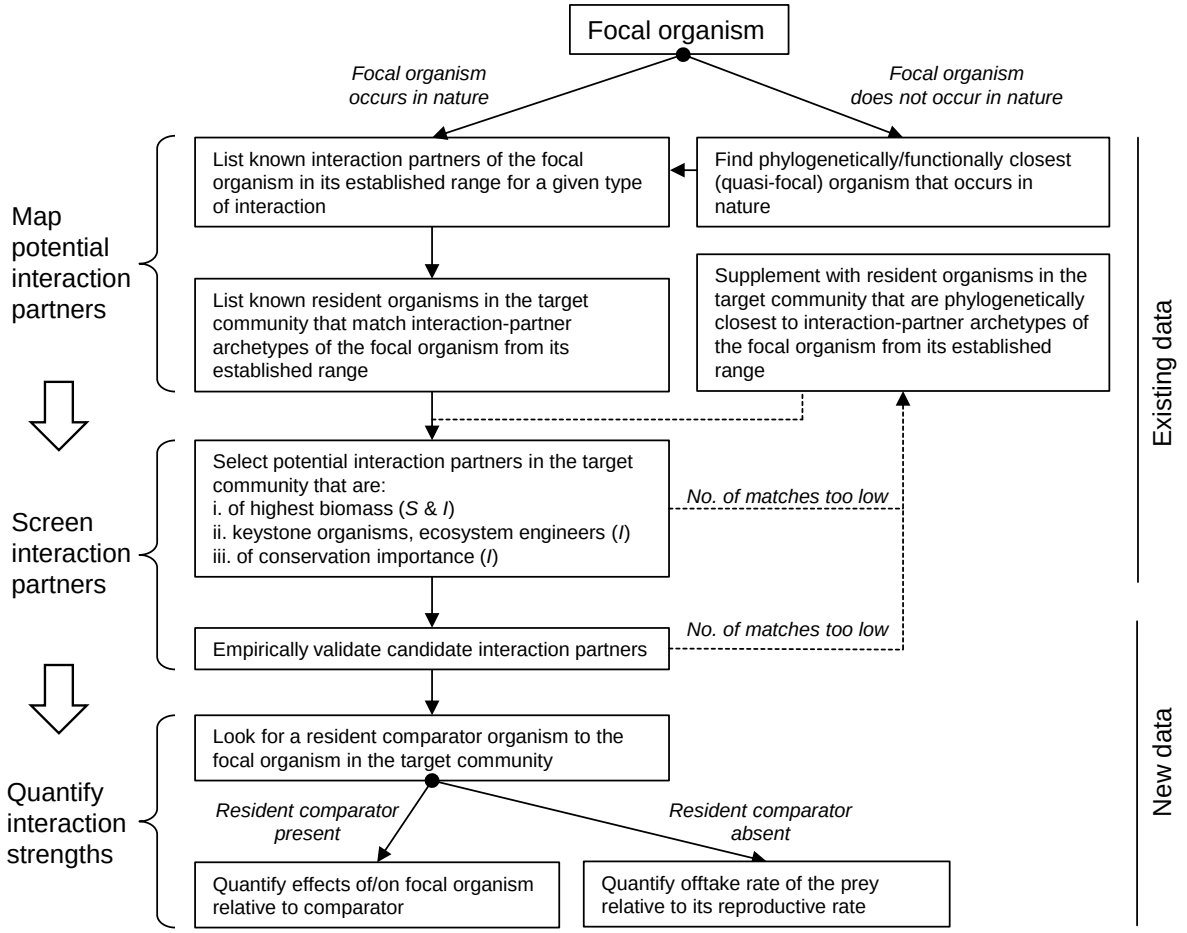
Focal organism
Focal organism occurs in nature
Focal organism does not occur in nature
List known interaction partners of the focal organism in its established range for a given type of interaction
Find phylogenetically/functionally closest (quasi-focal) organism that occurs in nature
Map potential interaction partners
List known resident organisms in the target community that match interaction-partner archetypes of the focal organism from its established range
Supplement with resident organisms in the target community that are phylogenetically closest to interaction-partner archetypes of the focal organism from its established range
Existing data
Select potential interaction partners in the target community that are:
i. of highest biomass (S & I)
ii. keystone organisms, ecosystem engineers (I)
iii. of conservation importance (I)
No. of matches too low
Screen interaction partners
Empirically validate candidate interaction partners
No. of matches too low
Look for a resident comparator organism to the focal organism in the target community
Quantify interaction strengths
Resident comparator present
Resident comparator absent
Quantify effects of/on focal organism relative to comparator
Quantify offtake rate of the prey relative to its reproductive rate
New data

Fig. 1

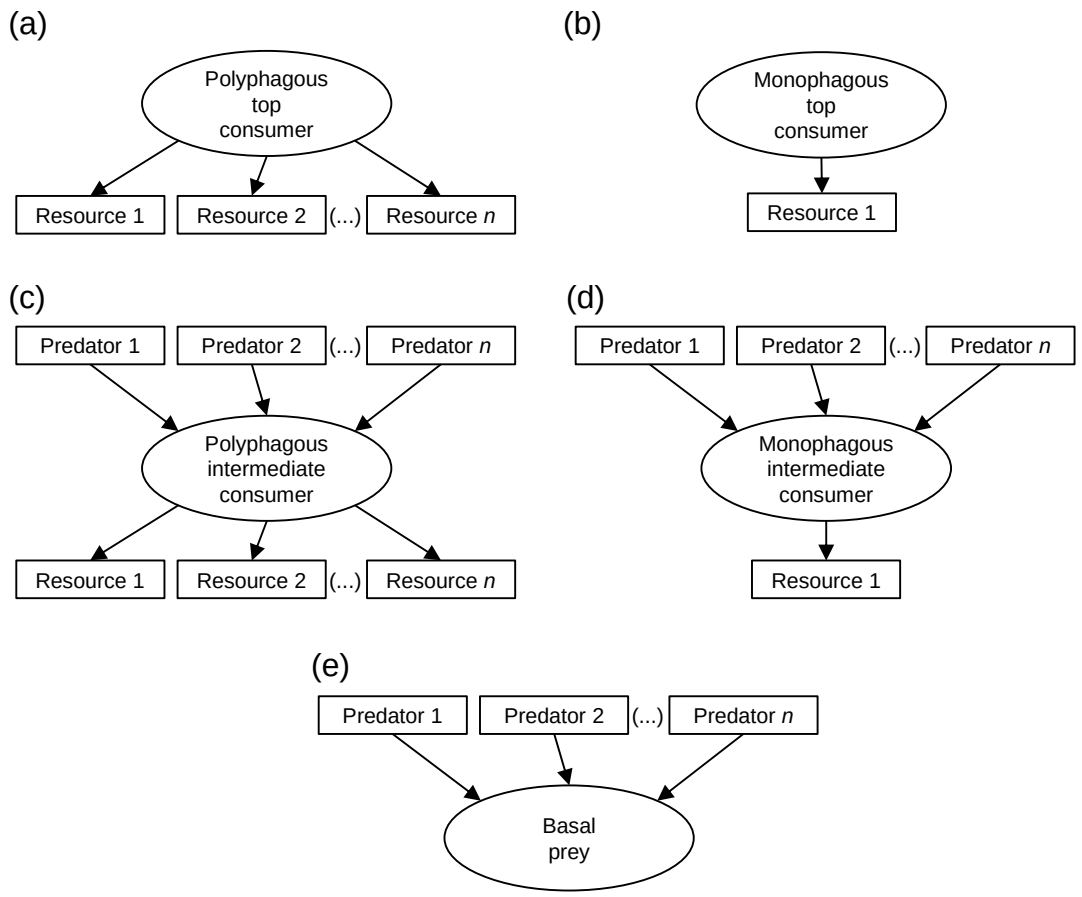
(a)
Polyphagous top consumer
Resource 1
Resource 2
(...)
Resource n
(b)
Monophagous top consumer
Resource 1
(c)
Predator 1
Predator 2
(...)
Predator n
Polyphagous intermediate consumer
Resource 1
Resource 2
(...)
Resource n
(d)
Predator 1
Predator 2
(...)
Predator n
Monophagous intermediate consumer
Resource 1
(e)
Predator 1
Predator 2
(...)
Predator n
Basal prey

Fig. 2

774 **Supporting Information**

775

776 A trophic interaction framework for identifying the invasive capacity of novel organisms

777

778 Marcin Penk, Wolf-Christian Saul, Jaimie T.A. Dick, Ian Donohue, Mhairi E. Alexander,

779 Stefan Linzmaier and Jonathan M. Jeschke

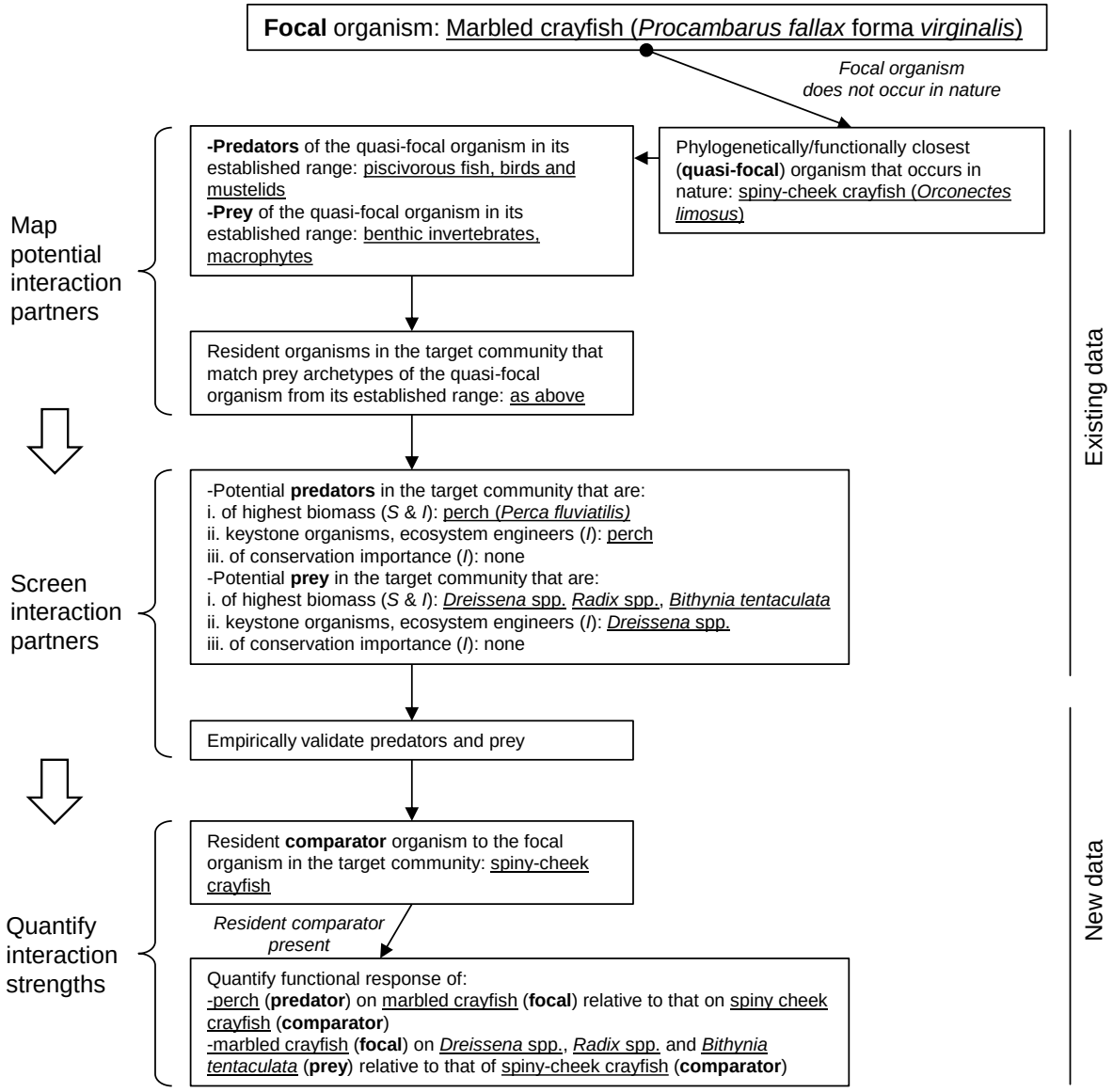

Fig. S1. Illustration of the framework for quantifying interaction strength of a focal organism with resident organisms in the target community, using an example of predator and prey selection for the marbled crayfish (*Procambarus fallax* forma *virginalis*) in a German low-land lake. *S* and *I* indicate prey categories relevant for the assessment of invasion success and ecological impacts, respectively. Quasi-focal organism is also the resident comparator in this example.

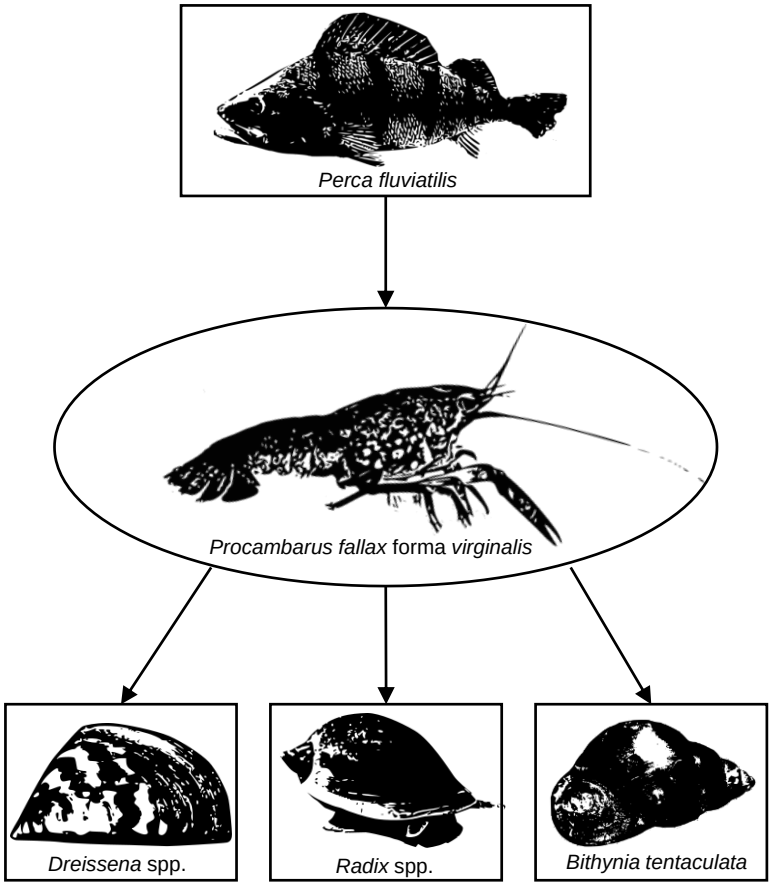

Fig. S2. Illustration of the interaction module structure for testing using an example of predator and prey (top and bottom boxes, respectively) selected for the marbled crayfish (central box) in a German low-land lake. Organisms are not to scale.

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805